EFFECT OF REINFORCER MAGNITUDE ON PERFORMANCE MAINTAINED BY PROGRESSIVE-RATIO SCHEDULES

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This experiment examined the relationship between reinforcer magnitude and quantitative measures of performance on progressive-ratio schedules. Fifteen rats were trained under a progressive-ratio schedule in seven phases of the experiment in which the volume of a 0.6-M sucrose solution reinforcer was varied within the range 6–300 μl. Overall response rates in successive ratios conformed to a bitonic equation derived from Killeen's (1994) Mathematical Principles of Reinforcement. The ''specific activation'' parameter, *a*, which is presumed to reflect the incentive value of the reinforcer, was a monotonically increasing function of reinforcer volume; the ''response time'' parameter, δ, which defines the minimum response time, increased as a function of reinforcer volume; the ''currency'' parameter, β, which is presumed to reflect the coupling of responses to the reinforcer, declined as a function of volume. Running response rate (response rate calculated after exclusion of the postreinforcement pause) decayed monotonically as a function of ratio size; the index of curvature of this function increased as a function of reinforcer volume. Postreinforcement pause increased as a function of ratio size. Estimates of *a* derived from overall response rates and postreinforcement pauses showed a modest positive correlation across conditions and between animals. Implications of the results for the quantification of reinforcer value and for the use of progressive-ratio schedules in behavioral neuroscience are discussed.

Key words: progressive-ratio schedule, reinforcer magnitude, Mathematical Principles of Reinforcement (MPR), lever press, rat

In a progressive-ratio schedule of reinforcement, the number of responses required to effect reinforcer delivery increases progressively (Hodos, 1961; Hodos & Kalman, 1963). The traditional measure of performance on this schedule is the ratio at which responding ceases for some predefined period (the ''breakpoint'': Baron, Mikorski, & Schlund, 1992; Hodos, 1961; Stafford & Branch, 1998), or alternatively the highest ratio completed within a time-limited experimental session (Aberman, Ward, & Salamone, 1998; Hamill, Trevitt, Nowend, Carlson, & Salamone, 1999; Ho, Body, Kheramin, Bradshaw, & Szabadi, 2003; Weatherley, King, & Uran, 2003).

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Tables of raw data from individual subjects and the parameters of the equations fitted to these data are available in the *supplementary materials* section of this article at PubMedCentral.

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The extensive use of progressive-ratio schedules in behavioral pharmacology derives from the widely held interpretation of the breakpoint or highest completed ratio as an index of the subject's motivational state (Barr & Philips, 1999; Bowman & Brown, 1998; Ferguson & Paule, 1997), or the incentive value of the reinforcer (Cheeta, Brooks, & Willner, 1995; Hodos, 1961). The finding that the breakpoint is sensitive to changes in deprivation level and reinforcer size (Ferguson & Paule, 1997; Sclafani & Ackroff, 2003; Skjoldager, Pierre, & Mittleman, 1993) is consistent with this interpretation. There are, however, significant problems with the use of the breakpoint as an index of motivation or reinforcer value, including the sensitivity of this measure to ''nonmotivational'' manipulations such as changes in the response requirement (Aberman et al., 1998; Skjoldager et al., 1993) and the ratio step size (Stafford & Branch, 1998). The breakpoint also suffers from the weakness that it is derived from a single time point during an experimental session; the data obtained during the rest of the session are ignored. Moreover, the definition of the breakpoint is somewhat arbitrary, and there is no general consensus as to the

period of time that must elapse before the subject may be said to have ceased responding.

A possible means of circumventing these problems is the application of a quantitative model of ratio-schedule performance (Killeen, 1994, 1998) which takes into account the response rate in each component ratio of the schedule. This model is derived from a general theory of schedule-controlled behavior, the Mathematical Principles of Reinforcement (MPR: Killeen, 1994), which is founded on fundamental postulates related to the incentive value of reinforcers, biological constraints on responding, and the efficiency with which particular reinforcement schedules couple operant responses to reinforcers. In the case of fixed-ratio schedules, in which N responses are required for each reinforcer delivery, response rate, R, is predicted by

$$R = \frac{\zeta}{\delta} - \frac{N}{a}, \quad \text{where } \zeta = 1 - (1-\beta)^N; \quad a, \delta > 0;\ 0 < \beta < 1. \quad (1)$$

The parameter β (''currency''), which represents the extent to which the strengthening effect of the reinforcer is focused on the most recent response, is intimately connected to the coupling characteristics of the schedule (defined by ζ); δ (''response time'') is the reciprocal of the maximum response rate; and a (''specific activation'') is the time for which a reinforcer is able to activate behavior. The last of these parameters, a, provides an index of reinforcer efficacy or ''value'' (Killeen, 1994; Killeen & Sitomer, 2003; Reilly, 2003). The link between the concepts of behavioral activation and incentive value arises from Killeen's (1982, 1985) observation that behavior is activated by reinforcers (incentives) in proportion to the rate of reinforcement; in Killeen's (1994) model, a specifies the duration of activation induced by a single reinforcer delivery. An illustration of the fit of Equation 1 to progressive-ratio schedule performance of one rat (rat 5 in the present experiment) is shown in Figure 1. Response rate rises rapidly to a peak and then falls more gradually towards zero. The slope of the descending limb of the function is the negative reciprocal of a, and the point of intersection of the (extrapolated) descending limb with the ordinate is the reciprocal of δ.

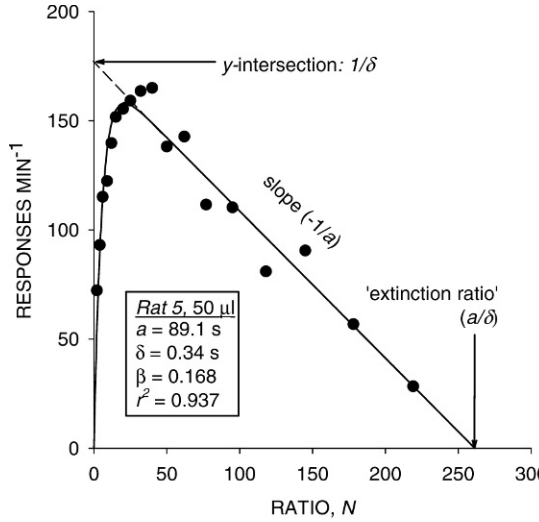

Fig. 1. Fit of Equation 1 to data obtained from one rat responding on a progressive- ratio schedule, illustrating the derivation of the parameters (rat 5, data from the 50 µl condition). *Ordinate:* response rate (R); *abscissa:* Response/reinforcer ratio (N). Points are mean overall response rates, averaged across ten sessions; the curve is defined by Equation 1 (parameter values: see inset). The (projected) point of intersection of the function with the ordinate is at R=1/δ; the slope of the descending limb of the function is $-1/a$.

Consistent with the interpretation of a as an index of reinforcer value, it has been demonstrated that this parameter is sensitive to manipulation of reinforcer size and quality (Bizo & Killeen, 1997; Reilly, 2003). Although Equation 1 was originally proposed as a model of fixed-ratio performance (Killeen, 1994), it also provides a good description of performance on progressive-ratio schedules, and has been used to evaluate the effects of centrally acting drugs (Ho et al., 2003; Mobini, Chiang, Ho, Bradshaw, & Szabadi, 2000; Reilly, 2003; Zhang, Rickard, Asgari, Body, Bradshaw, & Szabadi, 2005a, 2005b) and cerebral lesions (Bezzina, Body, Cheung, Hampson, Deakin, Anderson, et al., 2008; Kheramin, Body, Miranda Herrera, Bradshaw, Szabadi, Deakin, et al., 2005) on reinforcer efficacy.

The theoretical status of a in MPR has led to the suggestion that this parameter might be used to construct a quantitative scale of reinforcer value (Reilly, 2003). Consistent with this proposal, several studies have demonstrated that a is influenced by the size and quality of food reinforcers (Bezzina et al., 2008; Bizo & Killeen, 1997; Reilly, 2003). However, to

date, there has been no systematic exploration of the relationship between *a* and quantitative dimensions of reinforcer magnitude. The present experiment was an attempt to address this issue. Rats were exposed to progressive-ratio schedules using a wide range of reinforcer sizes (volumes of a standard sucrose solution). The relations between various features of progressive-ratio schedule performance, including the parameters of Equation 1, and reinforcer volume were examined.

As in previous studies (Bezzina et al., 2008; Ho et al., 2003; Kheramin et al., 2005; Mobini et al., 2000; Reilly, 2003; Zhang et al., 2005a, 2005b;), Equation 1 was fitted to the overall response rate calculated from the end of one reinforcer delivery until the start of the next. However it is well known that responding on ratio schedules, including progressive-ratio, consists of a relatively long postreinforcement pause followed by a rather uniform running response rate (Baron et al., 1992; Bizo & Killeen, 1997; Keesey & Goldstein, 1968; Mazur, 1983). In the present experiment the relations between all three measures of progressive-ratio schedule (overall response rate, postreinforcement pause and running response rate) and reinforcer volume were examined.

METHOD

Subjects

Fifteen experimentally naive female Wistar rats (Charles River UK Ltd.), approximately 4 months old and weighing 250–300 g at the start of the experiment, were used. They were housed under a constant cycle of 12 h light and 12 h darkness (light on 0600–1800 hours), and were maintained at 80% of their initial free-feeding body weights throughout the experiment by providing a limited amount of standard rodent diet after each experimental session. Tap water was freely available in the home cages.

Apparatus

The rats were trained in standard operant conditioning chambers (CeNeS Ltd, Cambridge, UK) of internal dimensions 25 × 25 × 22 cm. One wall of the chamber contained a central recess covered by a hinged clear Perspex (plexiglas) flap, into which a peristaltic pump could deliver a 0.6-M sucrose solution. Two apertures situated 5 cm above and 2.5 cm to either side of the recess allowed the insertion of motorized retractable levers (CeNeS Ltd, Cambridge, UK) into the chamber. The levers could be depressed by a force of approximately 0.2 N. The operant chamber was enclosed in a sound-attenuating chest with additional masking noise generated by a rotary fan. No houselight was present during the sessions. An Acorn microcomputer programmed in Arachnid BASIC (CeNeS Ltd, Cambridge, UK), located in an adjoining room, controlled the schedules and recorded the behavioral data.

Procedure

The experiment was carried out in accordance with UK regulations governing experiments on living animals. At the start of the experiment the food deprivation regimen was introduced and the rats were gradually reduced to 80% of their free-feeding body weights. Then they were trained to press the lever for the sucrose reinforcer (50 μl, 0.6 M), by presenting them with 50 reinforcers at 30-s intervals in the absence of the lever (three sessions), followed by exposure to a fixed-ratio (FR)-1 schedule for three sessions. Thereafter, they underwent daily training sessions under the progressive-ratio schedule. The progressive-ratio schedule was based on the following exponential progression: 1, 2, 4, 6, 9, 12, 15, 20, 25, 32, 40, 50, ..., derived from the formula $[(5\times e^{0.2n})-5]$, rounded to the nearest integer, where n is the position in the sequence of ratios (Roberts & Richardson, 1992). Sessions took place at the same time each day during the light phase of the daily cycle (between 0700 and 1400 hours) 7 days a week. At the start of each session, the lever was inserted into the chamber; the session was terminated by withdrawal of the lever 50 min later, irrespective of whether or not a breakpoint had been reached (see below).

The experiment consisted of seven phases, in which the volume of the sucrose reinforcer was systematically varied. The following volumes were employed in the seven phases: 6, 12, 25, 50, 100, 200 and 300 μl. The numbers of sessions were fixed for all subjects in each phase; no stability criterion was employed. All subjects were exposed to either 25 or 50 μl in the first phase, which continued for 60

sessions; the order of exposure to the remaining volumes in phases 2–7, each of which continued for 30 sessions, was counterbalanced across subjects.

Data Analysis

The data obtained during the last 10 sessions of training under the progressive-ratio schedule were used in the analysis. The breakpoint was defined as the last ratio to be completed before 5 min elapsed without any responding. In some cases, this was identical to the highest ratio completed in the session. However, in the case of larger reinforcer volumes, the breakpoint criterion was often not met within the 50-min session. Therefore, the highest completed ratio, rather than breakpoint, was adopted as the performance measure for analysis.

Overall response rate was calculated for each ratio; the total time taken to complete the ratio, including the postreinforcement pause, was used to calculate the overall response rate. Separate analyses were carried out on the running response rates, which were based on the ''run-time'' (time taken to complete a ratio, measured from the first response of the ratio).

Equation 1 was fitted to the overall response rate data obtained from each rat in each phase using an iterative least-squares method (SigmaPlot, Version 8.0), and the estimated values of the parameters β, δ and a were derived. In agreement with previous findings (Ho et al., 2003; Kheramin et al., 2005; Mobini et al., 2000; Zhang et al., 2005a,b), examination of the data revealed that Equation 1 provided a good description of the response rate data at low and intermediate ratios; however the low response rates generated under highest ratios did not always conform to the equation. Therefore the equation was fitted to each rat's data after exclusion of these low rates using the operational criterion described by Mobini et al. (2000). Points were removed successively, starting from the highest ratio completed, when the curve-fitting routine generated an abscissa intersection point (a/δ) which lay to the left of the rightmost empirical datum point; such an intersection implies a negative predicted response rate, which is impossible empirically, and specifically precluded by the model (see above, Equation 1). A fit was accepted when the predicted response rates for all the surviving data points had positive values. This procedure seldom eliminated more than one datum point from the data from individual rats.

Equation 1 was found to provide a poor fit to the running rate data, which could, however, be well described by a three-parameter logistic function:

$$R = R_i / (1 + [N/b]^c), \tag{2}$$

where R_i is the projected initial running rate at $N = 0$, b is the ratio at which $R = R_i/2$, and the exponent c modulates the curvature of the function.

The parameters of Equations 1 and 2 derived for the individual rats were analysed by analysis of variance with reinforcer volume as a within-subject factor. Hyperbolic functions were fitted to the relations between a (Equation 1) and b (Equation 2) and reinforcer volume, q:

$$a = a_{MAX} \cdot q/(Q + q) \tag{3a}$$

$$b = b_{MAX} \cdot q/(Q + q), \tag{3b}$$

where a_{MAX} and b_{MAX} are the asymptotes of the functions and Q is a parameter expressing the reinforcer volume corresponding to the half-maximal values of a or b.

Postreinforcement pauses (PRP) were analysed using the equation proposed by Bizo and Killeen (1997):

$$PRP = \frac{k \cdot N}{\frac{1}{\delta} - \frac{N}{a}} \tag{4}$$

where N, δ and a have the same definitions as in Equation 1, and k is a parameter expressing the ratio of the postreinforcement pause to the interreinforcer interval.

Goodness of fit of all fitted functions was expressed as the proportion of variance accounted for by the function (r^2).

RESULTS

Highest Completed Ratio

Figure 2 shows the group mean highest completed ratios (± SEM); the data from the individual rats are shown in Table 1. There was an asymptotic rise of the highest completed ratio as a function of increasing reinforcer

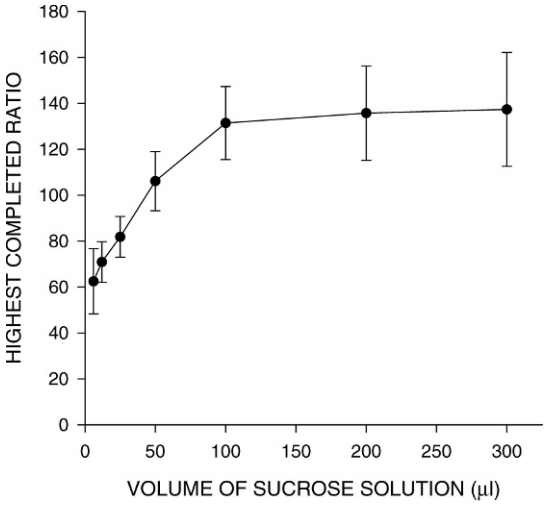

Fig. 2. Relationship between the highest completed ratio and reinforcer volume. *Ordinate:* Highest completed ratio; *abscissa:* volume of 0.6 M sucrose solution, µl. Points are group mean data; bars represent SEM.

volume. This was reflected in a significant effect of reinforcer volume, $F(6, 84) = 13.3$, $p < .001$.

Overall Response Rate: Analysis Using MPR (Equation 1)

The group mean data are shown in Figure 3 (left-hand panel); the raw data from the individual rats are available online in the supplementary data file for this article. In the case of each reinforcer volume, response rate rose rapidly to a peak and then declined progressively as a function of increasing ratio. Higher reinforcer volumes were associated with lower peak response rates and flatter declining limbs of the response rate function. The fits of Equation 1 to the group mean data are shown in the figure; in the case of each reinforcer volume, the function accounted for more than 88% of the data variance. The parameters of the functions fitted to the individual rats are presented in the online supplementary data file; in general, the fitted functions accounted for about 90% of the data variance.

The relations between each parameter of Equation 1 and the volume of the reinforcer are shown in Figure 4. All three parameters were significantly affected by reinforcer volume.

*"Specific activation", a (*Figure 4A*).* The value of this parameter increased steadily as a function of reinforcer volume, showing some tendency to asymptote at the highest reinforcer volume. The rectangular hyperbolic function (Equation 3a) accounted for > 95% of the variance of the group mean data (see broken line in Figure 4A). There was a significant effect of reinforcer volume on *a*, $F(6, 84) = 54.9$, $p < .001$.

*"Response time", δ (*Figure 4B*).* With volumes up to 50 µl, the mean value of the parameter was between 0.49 and 0.58 s, and showed little variation as a function of reinforcer volume. However, with volumes of

Table 1

Highest completed ratios obtained by individual rats.

	Volume of sucrose solution (µl)						
Rat	6	12	25	50	100	200	300
1	44	89	103	103	154	194	149
2	25	34	53	49	56	56	58
3	61	76	87	80	102	79	102
4	210	102	132	149	266	313	382
5	77	61	117	211	249	269	297
6	49	68	106	159	150	156	161
7	52	82	87	125	155	102	76
8	31	32	34	64	67	72	71
9	62	63	62	91	91	96	79
10	21	26	38	66	94	63	62
11	24	80	83	110	120	100	93
12	71	117	80	86	120	146	179
13	27	43	55	53	96	80	54
14	17	41	45	63	78	88	90
15	166	150	146	185	172	222	208

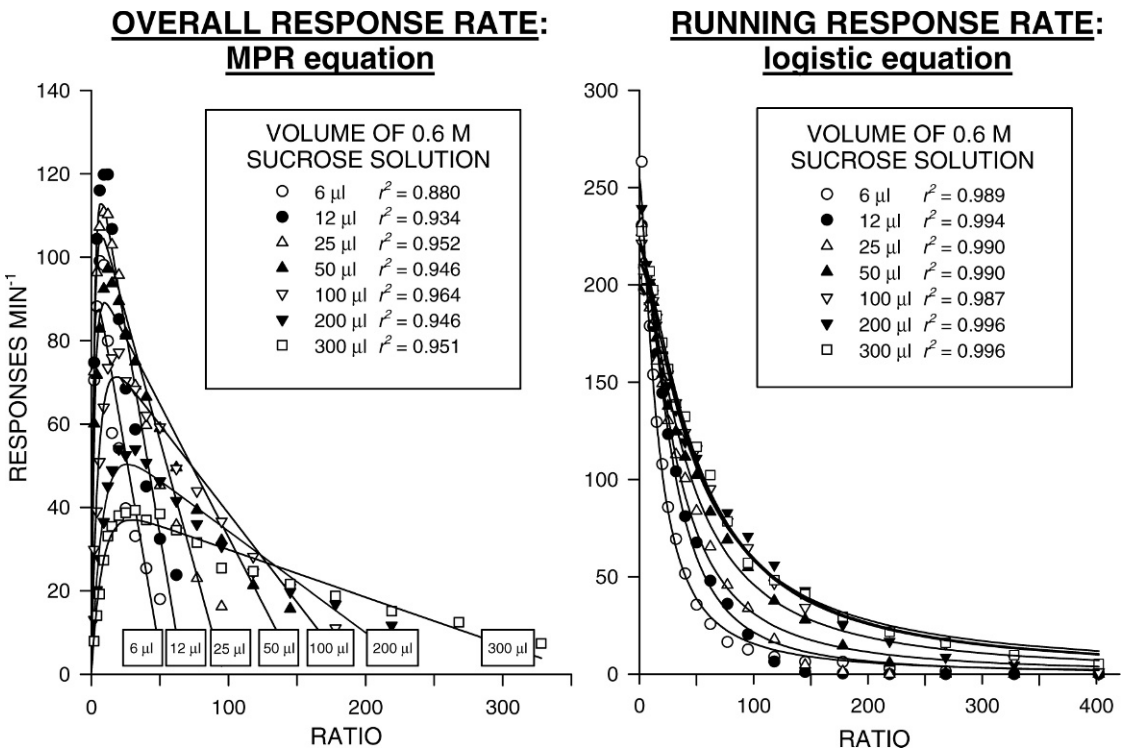

Fig. 3. Response rates in the progressive-ratio schedule. *Left panel:* overall response rate; *right panel:* running response rate. *Ordinates:* response rate (responses minute^{-1}); *abscissae:* ratio, *N*. Points are group mean data for each reinforcer volume (see inset). Fits of Equation 1 (left panel) and Equation 2 (right panel) are shown for each data set; goodness of fit (r^2) values are shown in the inset.

100 µl and above, δ increased progressively, with no indication of an asymptote within the range of volumes tested. There was a significant effect of reinforcer volume on δ, $F(6, 84) = 25.9$, $p < .001$.

*"Currency", β (*Figure 4C*).* The value of the parameter declined progressively as a function of volume, approaching an asymptote of approximately 0.1 at volumes of 200 and 300 µl. There was a significant effect of reinforcer volume on β, $F(6, 84) = 22.4$, $p < .001$.

Running Response Rate: Analysis Using Equation 2

The group mean data are shown in Figure 3 (right-hand panel); the raw data from the individual rats are presented in the online supplementary data file. In the case of each reinforcer volume, running response rate was highest at the lowest ratios, falling monotonically as a function of increasing ratio. Higher reinforcer volumes were associated with more gradual declines of response rate. The fits of Equation 2 to the group mean data are shown in the figure; in the case of each reinforcer volume, the function accounted for more than 98% of the data variance. The parameters of the functions fitted to the data from the individual rats are presented in the online supplementary data file; in general, the fitted functions accounted for about 90% of the data variance, although the function could not be fitted to five out of the seven data sets from one rat (rat no. 15) and one set from another rat (rat no. 14). The relations between each parameter of Equation 2 and the volume of the reinforcer are shown in Figure 5.

*Initial running rate, R_i (*Figure 5A*).* There was no systematic effect of reinforcer volume on R_i, $F(6, 72) = 1.1$, $p > .1$.

*Decay parameter, b (*Figure 5B*).* The value of *b* increased monotonically towards an asymptote. The rectangular hyperbolic function

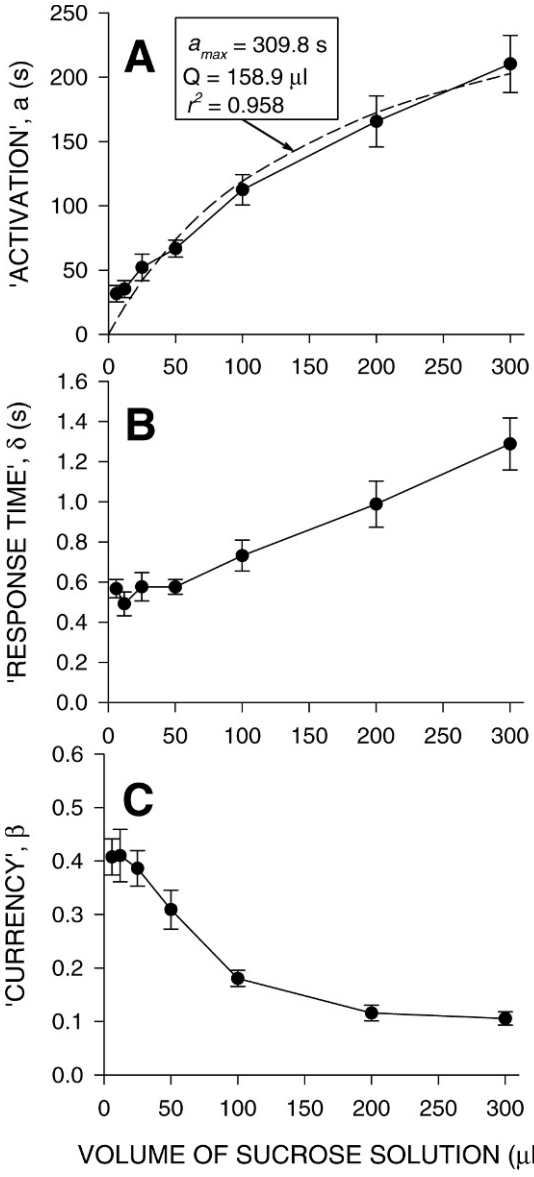

Fig. 4. Parameters of Equation 1 derived for overall response rates on the progressive-ratio schedule. *Ordinates:* value of parameter; *abscissae:* volume of 0.6 M sucrose solution. Points are group mean data; bars represent SEM. Data from individual rats are given in the supplemental section of this article at PubMedCentral. *A.* Activation parameter, *a* (s); broken line is the best-fit rectangular hyperbola (Equation 3a). *B.* Response time parameter, δ (s). *C.* Currency parameter, β.

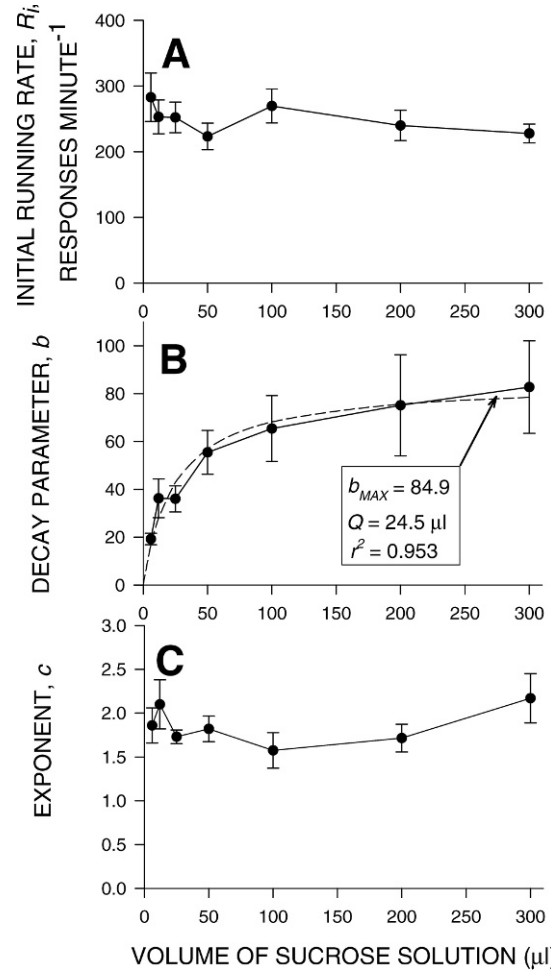

Fig. 5. Parameters of Equation 2 derived for running response rates on the progressive-ratio schedule. *Ordinates:* value of parameter; *abscissae:* volume of 0.6 M sucrose solution. Points are group mean data; bars represent SEM. Data from individual rats are given in the online supplementary data file. *A.* Initial response rate, R_i (responses minute^{-1}). *B.* Curvature parameter of logistic function, *b*; broken line is the best-fit rectangular hyperbola (Equation 3b). *C.* Exponent of logistic function, *c*.

(Equation 3b) accounted for more than 93% of the variance of the group mean data (see broken line in Figure 5B). The effect of reinforcer volume on *b* was statistically significant, $F(6, 72) = 5.9$, $p < .001$.

Exponent, c (Figure 5C). There was no systematic effect of reinforcer volume on *c*, $F(6, 72) = 1.2$, $p > .1$.

Postreinforcement Pause: Analysis Using Equation 4

Postreinforcement pause increased as a function of ratio size (Figure 6); the raw data from the individual rats are presented in the online supplementary data file. At all ratios, there was a tendency for larger reinforcer

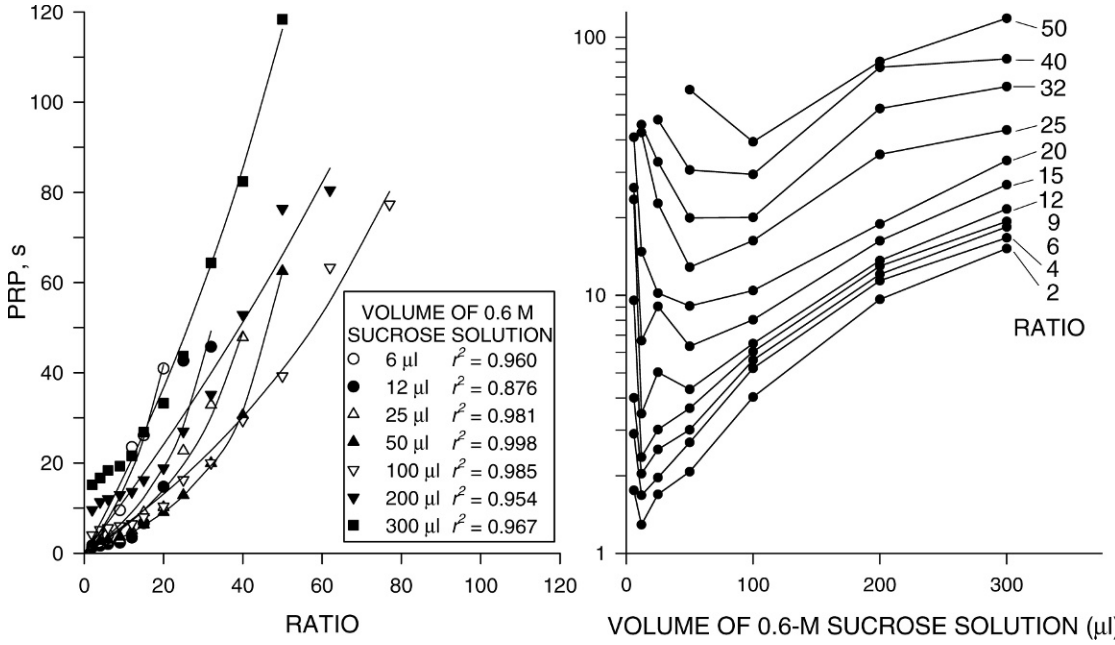

Fig. 6. Postreinforcement pauses. *Left panel.* Relation between postreinforcement pause (s) and ratio for each volume of sucrose. Points are group mean data (see inset). The curves are best-fit functions defined by Equation 4. *Right panel.* Relation between postreinforcement pause (s, on logarithmic scale) and reinforcer volume (µl) for ratios between 2 and 50.

volumes to be associated with longer postreinforcement pauses (see Figure 6, right-hand panel). The fits of Equation 4 to the group mean data are shown in the figure (left-hand panel); in the case of each reinforcer volume, the function accounted for more than 87% of the data variance. The parameters of the functions fitted to the individual rats are presented in the online supplementary data file; in general, the fitted functions accounted for about 90% of the data variance. However, the function could not be fitted to one or more of the data sets from 5 of the 15 rats.

The relations between each parameter of Equation 4 and the volume of the reinforcer are shown in Figure 7.

*Activation parameter, a (*Figure 7A*).* The value of this parameter increased as a function of reinforcer volume, showing some tendency to asymptote at the highest reinforcer volume. The rectangular hyperbolic function (Equation 3a) provided a modest description of this relation (see broken line in Figure 4, upper panel), accounting for less than 70% of variance in the group mean data. The effect of reinforcer volume on a was statistically significant, $F(6, 60) = 3.2$, $p < .01$.

*Response time parameter, δ (*Figure 7B*).* There was no systematic effect of reinforcer volume on δ, $F(6, 60) = 1.8$, $p > .1$.

*PRP/interreinforcer-interval ratio parameter, k (*Figure 7C*).* This parameter showed a U-shaped relation to reinforcer volume, assuming its lowest values at intermediate volumes. The effect of reinforcer volume on k was statistically significant, $F(6, 60) = 3.5$, $p < .01$.

Correlations Between Parameter Estimates

Specific activation, a. Estimates of a derived from Equation 1 (overall response rates) and Equation 4 (postreinforcement pauses) showed a moderate positive correlation, $r = 0.572$, $p < .001$. The correlation survived controlling for differences between rats, $r_{partial} = 0.570$, $p < .001$, and controlling for differences between reinforcer volumes, $r_{partial} = 0.450$, $p < .001$. Estimates of a were significantly correlated with the index of curvature of the running rate equation (*b,* Equation 2), $r = 0.584$, $p < .001$. The correlation survived controlling for differences between rats, $r_{partial} = 0.548$, $p < .001$, and controlling for differences between reinforcer volumes, $r_{partial} = 0.507$, $p < .001$.

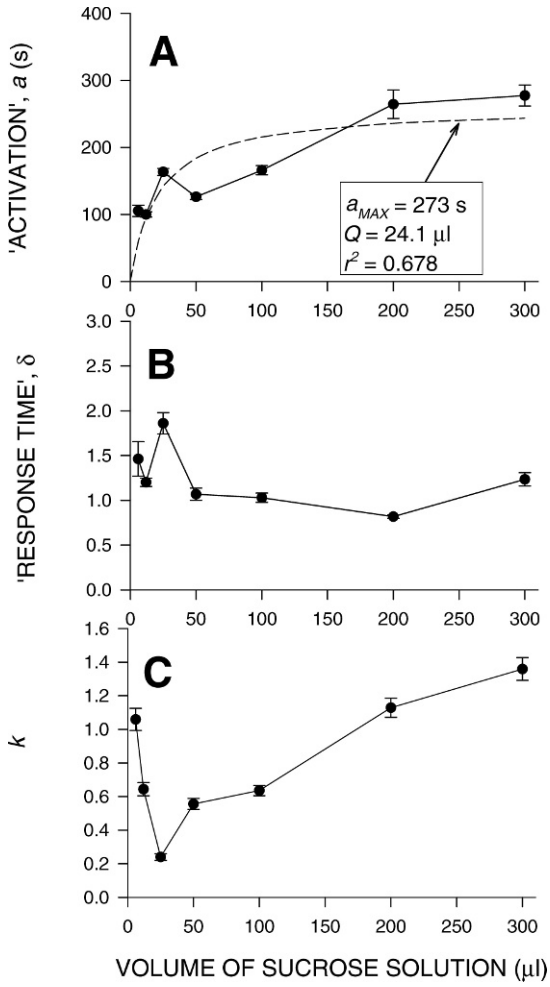

Fig. 7. Parameters of Equation 4 derived for postreinforcement pauses on the progressive-ratio schedule. *Ordinates:* value of parameter; *abscissae:* volume of 0.6 M sucrose solution. Points are group mean data; bars represent SEM. Data from individual rats are given in the online supplementary data file. *A.* Activation parameter, a (s); broken line is the best-fit rectangular hyperbola (Equation 3a). *B.* Response time parameter, δ (s). *C.* Parameter expressing the ratio of postreinforcement pause to interreinforcer interval, k.

Response time, δ. Estimates of δ derived from Equations 1 and 4 were not significantly correlated with one another, $r = 0.135$, $p > .1$.

DISCUSSION

The highest completed ratio increased monotonically as a function of reinforcer volume, approaching an asymptote at volumes above 100 µl. It should be noted, however, that this asymptote is an artifact of the 50-min constraint imposed on the session length, because responding often failed to reach a breakpoint by the end of the session in the case of higher reinforcer volumes. This problem could have been obviated by allowing each session to continue until a breakpoint was attained. However, this policy has its own drawbacks, particularly in behavioral pharmacology experiments, where accurate pharmacokinetic information about the drug being tested is often not available. As has been noted by several authors, reliance on a single time point determined by the subject's persistence in responding can be problematic when examining the effects of drugs with short plasma half-lives (Arnold & Roberts, 1997; Rowlett, 2000; Stafford & Branch, 1998).

Overall response rates showed a bitonic relation with ratio size, increasing to a peak and then declining progressively. This trend was apparent in all the subjects (see the online supplementary data file) as well as in the group mean data (Figure 3, left panel). In agreement with many previous experiments (Bezzina et al., 2008; Ho et al., 2003; Kheramin et al., 2005; Killeen, Posadas-Sanchez, Johansen, & Thrailkill, in press; Mobini et al., 2000; Reilly, 2003; Zhang et al., 2005a, 2005b) overall response rates in the progressive-ratio schedule were well described by Equation 1, the function derived in MPR to account for performance on fixed-ratio schedules (Killeen, 1994). It must be acknowledged that the application of Equation 1 to performance maintained under progressive-ratio schedules ignores an important difference between fixed- and progressive-ratio schedules. Unlike fixed-ratio schedules, in which the response/reinforcer ratio remains constant throughout each experimental session, progressive-ratio schedules prescribe a response/reinforcer ratio that increments progressively as a function of successive reinforcer deliveries. It is likely that responding in each ratio is influenced by the previous ratio, and possibly also by the upcoming ratio (Baron & Derenne, 2000). This could distort the relation between response rate and response/reinforcer ratio specified by Equation 1 (see below). Nevertheless, the present results, as well as those of many previous experiments, attest to the adequacy of Equation 1 as a descriptor of overall response rates in progressive-ratio

schedules, both at the level of group mean data and at the level of the individual animal.

As expected, the ''specific activation'' parameter, *a*, was monotonically related to reinforcer size. This is consistent with the interpretation of this parameter as a measure of the incentive value of the reinforcer (Killeen, 1994), and with Reilly's (2003) suggestion that *a* may be used to construct a quantitative scale of reinforcer value (see below for further discussion).

The ''minimum response time'' parameter, δ, increased systematically as a function of reinforcer volume. This is consistent with previous findings (Bezzina et al., 2008; Bizo, Kettle, & Killeen, 2001). It is likely that this effect reflects a greater contribution of postprandial behavior to postreinforcement pauses in the case of larger reinforcer volumes.

The ''currency'' parameter, β, declined as a function of reinforcer volume, again consistent with previous results (Bezzina et al., 2008; Bizo, Kettle, & Killeen, 2001). This corresponds to a rightward displacement of the peak of the response rate function as a function of reinforcer volume (see Killeen, 1994). A modification of MPR (Bizo et al., 2001) offers a theoretical explanation for this observation. In the original formulation of MPR (Killeen, 1994), the relation between response–reinforcer coupling, ζ, in ratio schedules and the currency parameter, β (see Equation 1), is based on the assumption that each reinforcer effects complete ''erasure'' of short-term memory for recent responses. In Bizo et al.'s (2001) modified model, the degree of erasure is assumed to increase as a function of reinforcer size; this is reflected in the degree of coupling, and hence in the value of β, as defined by Equation 1.

Equation 1 did not yield a good account of running response rates, which were, however, well described by a three-parameter logistic function (Equation 2). This finding is at variance with the prediction of MPR (Killeen, 1994) that the same function should describe overall and running response rates. Interestingly, the maximal response rate parameter, R_i, did not vary systematically with reinforcer volume, in agreement with the speculation that the systematic relation between δ (Equation 1) and reinforcer volume was principally attributable to the effect of prolonged postreinforcement pausing in the case of larger volumes (see above). The running-rate function was displaced progressively to the right as a function of increasing reinforcer volume, this being reflected in the index of curvature of the running-rate function, *b*, which defines the response/reinforcer ratio at which running rate is half its maximal value. This index increased systematically with reinforcer volume. The exponential term in the logistic equation, *c*, was unrelated to reinforcer volume.

A striking feature of the running response rate data is the concave appearance of the relation between response rate and response/reinforcer ratio, which is clearly incompatible with the linear decline in response rate demanded by Equation 1. Some concavity is also apparent in the overall response rate functions, especially in the case of lower reinforcer volumes. This concavity has been noted previously; it is not a feature of repending on fixed- and variable-ratio schedules and is strongly influenced by the nature of the ratio progression (arithmetic, geometric) in the schedule (Killeen et al., in press). A recent extension of MPR that deals specifically with progressive-ratio schedules by Killeen et al. accommodates concavity of the response rate function using an additional parameter to represent the overall reinforcing context afforded by the schedule. However Killeen et al.'s extended model of progressive-ratio schedule performance treats overall and running response rates similarly, and it remains unclear why the running response rate data from the present experiment should exhibit a much greater degree of concavity than the corresponding overall response rate data.

In agreement with previous findings, the duration of the postreinforcement pause increased as a function of ratio size (Bizo & Killeen, 1997; Keesey & Goldstein, 1968; Mazur, 1983), and also as a function of reinforcer volume (Baron et al., 1992). These trends are apparent in the individual subject data as well as in the group mean data (Figure 6). In the case of the group mean data and the majority of the individual-subject data sets, the relation between postreinforcement pause and ratio size conformed approximately to the function proposed by Bizo and Killeen (Equation 4).

Equation 4, like Equation 1, expresses the activation and response time parameters of

MPR (a and δ, respectively). It was therefore of interest to examine whether the two estimates of each parameter were in agreement. There was a moderately strong correlation between the two estimates of a, although the numerical values of the two estimates differed quite widely in some cases. Surprisingly, however, there was no significant correlation between the estimates of δ derived from the response rate and postreinforcement pause data.

Implications for the Measurement of Reinforcer Value

The quantification of relative reinforcer value has a long history in behavior analysis (Baum, 1974; Davison & McCarthy, 1988; de Villiers & Herrnstein, 1976; Herrnstein, 1961, 1970). However, the quantification of the absolute values of reinforcers is less well developed. Herrnstein's (1970) hyperbolic response strength equation has provided a basis for quantifying the values of food and water reinforcers, and for identifying the effects of drug treatment and cerebral lesions on reinforcer value (Bradshaw & Szabadi, 1989; Heyman & Monaghan, 1987, 1994), and analogous methods have been used to quantify the efficacy of electrical brain stimulation reward (Shizgal, 1997; Stellar & Rice, 1989). Relatively little attention has been paid to the relation between reinforcer magnitude and value, although several authors have argued that the relation is likely to be nonlinear (e.g., Ho, Mobini, Chiang, Bradshaw, & Szabadi, 1999; Killeen, 1985; Vaughan 1985; Shizgal, 1997). In Ho et al.'s model, in which instantaneous reinforcer value combines multiplicatively with hyperbolic delay discounting (Ainslie, 1975; Mazur, 1987), value is assumed to be a hyperbolic function of reinforcer magnitude. Inasmuch as the parameter a is a valid measure of instantaneous reinforcer value, this assumption leads to the prediction that a should be hyperbolically related to reinforcer volume. The data shown in Figure 4A are consistent with this prediction, although the data would no doubt be compatible with other nonlinear functions.

The modest correlation between estimates of a derived from overall response rate and postreinforcement pause, together with the much weaker relation between reinforcer volume and estimates of a derived from postreinforcement pauses compared to estimates of the same parameter derived from overall response rates, suggests that these two methods of estimating a may not be equivalent. Further work is needed to establish the extent to which the two approaches to estimating a are mutually compatible; for example, it would be of interest to see whether the two estimates of this parameter are affected similarly by centrally acting drugs and cerebral lesions. Interestingly, estimates of a derived from overall response rates were quite strongly correlated with the index of curvature, b, of the logistic running response rate function (Equation 2). Although Equation 2 is purely empirical, and has no theoretical status in MPR, these data suggest that b, like a may constitute a useful index of reinforcer value.

Implications for Behavioral Neuroscience

The progressive-ratio schedule is a popular tool for assessing the effects of centrally-acting drugs and cerebral lesions on reinforcer efficacy. Unfortunately, the traditional measure of reinforcer efficacy derived from performance on this schedule, the breakpoint or highest completed ratio, is prone to a number of shortcomings, not least of which is the confounding of effects on reinforcer efficacy with effects on response capacity (see Introduction). MPR offers a way of dissociating effects on incentive and motor processes, as these two processes are expressed by separate parameters of Equation 1 (a and δ, respectively). This approach has enabled the effects of different classes of antipsychotic drugs (''conventional'' antipsychotics, such as haloperidol, and ''atypical'' antipsychotics, such as clozapine) to be distinguished. Unlike conventional antipsychotics, which tend either to reduce a or to have no effect on this parameter (Mobini et al., 2000; Zhang et al., 2005b), atypical antipsychotics increase a, consistent with the hypothesis that these drugs enhance motivation for food reinforcers (Mobini et al., 2000; Zhang et al., 2005a, 2005b).

Some recent observations of the effects of cerebral lesions on progressive-ratio schedule performance may offer a promise of convergence between MPR and models of choice behavior, such as Ho et al.'s (1999) mutiplicative hyperbolic model. Destruction of the orbital prefrontal cortex in rats resulted in a reduction of a (Kheramin et al., 2005), whereas destruction of the core of the nucleus

accumbens had no effect on this parameter (Bezzina et al., 2008), suggesting that the orbital prefrontal cortex, but not the nucleus accumbens core, is involved in determining instantaneous reinforcer value. These findings coincide with observations of the effects of the same lesions on intertemporal choice behavior. Lesions of the orbital prefrontal cortex (Kheramin et al., 2002), but not lesions of the nucleus accumbens core (Bezzina et al., 2007), increased the slope of the linear function relating the indifference delay to the larger of two reinforcers to the delay imposed on the smaller reinforcer (see also Mazur, 2006). According to Ho et al. (1999), an increase in the slope of the indifference function signifies an increase in the ratio of the values of the two reinforcers, which, based on the assumption of a hyperbolic relation between reinforcer magnitude and value, implies a reduction of the absolute values of both reinforcers (Kheramin et al., 2005). Thus, the effects of the lesions on such disparate behaviors as response rates in progressive-ratio schedules and choice between delayed reinforcers in discrete-trial schedules can lead to coherent conclusions about the effects of lesions on reinforcer value.

To date, our knowledge about the role of different brain structures in regulating reinforcer value is essentially qualitative in nature. For example, the evidence outlined above indicates that orbital prefrontal cortex may be involved in determining instantaneous reinforcer value, but does not address such questions as whether this structure sets an upper limit to reinforcer value or whether it defines the organism's sensitivity to reinforcer magnitude. The use of formal models such as MPR to construct a numerical scale of reinforcer value (Killeen, 1994; Reilly, 2003) offers the prospect of placing neurobehavioral studies of reinforcement mechanisms on a more quantitative footing.

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